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RESEARCH ARTICLE

Signal-specific amplitude adjustment to noise in common bottlenose dolphins (*Tursiops truncatus*)

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ABSTRACT

Anthropogenic underwater noise has increased over the past century, raising concern about the impact on cetaceans that rely on sound for communication, navigation and locating prey and predators. Many terrestrial animals increase the amplitude of their acoustic signals to partially compensate for the masking effect of noise (the Lombard response), but it has been suggested that cetaceans almost fully compensate with amplitude adjustments for increasing noise levels. Here, we used sound-recording DTAGs on pairs of free-ranging common bottlenose dolphins (*Tursiops truncatus*) to test (i) whether dolphins increase signal amplitude to compensate for increasing ambient noise and (ii) whether adjustments are identical for different signal types. We present evidence of a Lombard response in the range 0.1–0.3 dB per 1 dB increase in ambient noise, which is similar to that of terrestrial animals, but much lower than the response reported for other cetaceans. We found that signature whistles tended to be louder and with a lower degree of amplitude adjustment to noise compared with non-signature whistles, suggesting that signature whistles may be selected for higher output levels and may have a smaller scope for amplitude adjustment to noise. The consequence of the limited degree of vocal amplitude compensation is a loss of active space during periods of increased noise, with potential consequences for group cohesion, conspecific encounter rates and mate attraction.

KEY WORDS: Cetacean, Signature whistle, Communication, Anthropogenic noise, Masking, Lombard response

INTRODUCTION

Marine environments have seen a steady increase in anthropogenic underwater noise over the past century (Andrew et al., 2002; Hildebrand, 2009; McDonald et al., 2006; Merchant et al., 2016), and noise is now recognized as an environmental pollutant of global concern (Van der Graaf et al., 2012). Many marine animals have evolved to rely on hearing as one of their primary senses, and sound has come to play a fundamental role in vital behaviours as diverse as foraging, predator detection, communication and navigation (King and Janik, 2015; Simpson et al., 2005; Vasconcelos et al., 2012). With this in mind, there is growing concern among the scientific community, regulatory agencies and the public as to how anthropogenic noise pollution might affect marine animals (Boyd et al., 2011; Erbe et al., 2018).

At present, there is substantial evidence that anthropogenic noise can have detrimental effects on a variety of marine animals (Slabbekoorn et al., 2010; Weilgart, 2007). High-intensity sound sources can have serious consequences including fatal injury or strandings (Frantzis, 1998; Parsons et al., 2008; Simmonds and Lopez-jurado, 1991) or lead to temporarily or permanently elevated hearing thresholds (Kastak et al., 2005; Mooney et al., 2009; Smith et al., 2004). At lower exposure levels, anthropogenic noise may affect behavioural patterns (Nowacek et al., 2007; Samson et al., 2016), which can be associated with fitness consequences and eventually population-level effects (Nabe-Nielsen et al., 2018; New et al., 2014). Anthropogenic noise may also interfere with the ability of marine animals to detect biologically relevant sounds – an effect termed masking (American National Standards Institute, 2008; Erbe et al., 2016b). Studies have shown that masking by anthropogenic noise can cause failure to detect and discriminate a range of important sounds used for localization of prey (Schaub et al., 2008), parent–offspring interactions (Lucass et al., 2016) and predator recognition (Templeton et al., 2016), among others. Thus, increasing noise may compromise detection of acoustic signals and effectively reduce the conspecific detection range or active space (Marten and Marler, 1977).

Masking is a universal feature of all sensory systems. Underwater soundscapes typically consist of noise generated by wind, waves and precipitation as well as biological sounds, such as fish choruses or snapping shrimp (Erbe et al., 2016a), all of which can vary greatly with both time and location. Consequently, many species have evolved mechanisms to mitigate effects of masking and ensure efficient communication across a wide span of ambient noise levels (Erbe et al., 2016b). Among these are vocal adaptations of the sender, including changes in signal type (Dunlop et al., 2010), changes in signalling activity such as timing or redundancy, or modifications of certain signal features such as frequency or amplitude (Hotchkin and Parks, 2013; Tyack and Janik, 2013). One such modification is the increase of signal amplitude in response to a perceived increase in ambient noise – a mechanism known as the Lombard response (Brumm and Zollinger, 2011; Lombard, 1911). In humans, the magnitude of the Lombard response has been shown to vary according to experimental design, but increases in vocal amplitude generally range from 0.05 to 0.4 dB per 1 dB increase in noise level (Table 1; Garnier et al., 2010; Hotchkin and Parks, 2013). A similar Lombard response magnitude in the range of 0.2 to 0.8 dB per 1 dB increase in noise level has been demonstrated for

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Table 1. The Lombard response magnitude measured across taxonomic groups

Taxonomic group	Species	Lombard response magnitude (dB/dB)	Reference
Primates	Human [speech]	0.05–0.2	Lane and Tranel, 1971
		0.12–0.38	Garnier et al., 2010
		0.14–0.41	Cynx et al., 1998
	Long-tailed macaque (*Macaca fascicularis*)	0.2	Sinnott et al., 1975
	Pig-tailed macaque (*Macaca nemestrina*)	0.2	Sinnott et al., 1975
	Common marmoset (*Callithrix jacchus*)	0.3–0.75	Brumm et al., 2004
	Cotton-top tamarin (*Saguinus oedipus*)	0.35–0.63	Egnor and Hauser, 2006
	Grey mouse lemur (*Microcebus murinus*)	0.2–0.22	Schopf et al., 2016
Bats	Free-tailed bat (*Tadarida brasiliensis*)	0.43 (echolocation)	Tressler and Smotherman, 2009
	Pale spear-nosed bats (*Phyllostomus discolor*)	0.1 (echolocation)	Luo et al., 2015
Cetaceans	Humpback whale (*Megaptera novaeangliae*)	0.9	Dunlop et al., 2014
		0.81	Fournet et al., 2018
	Right whale (*Eubalaena glacialis*)	1	Parks et al., 2011a
	Killer whale (*Orcinus orca*)	1	Holt et al., 2009
	Beluga whale (*Delphinapterus leucas*)	0.88	Scheifele et al., 2005
	Bottlenose dolphin (*Tursiops truncatus*)	0.1–0.3	This study
Birds	Zebra finch (*Taeniopygia guttata*)	0.3–0.49	Cynx et al., 1998
	Great tits (*Parus major*)	0.28	Zollinger et al., 2017
	Nightingale (*Luscinia megarhynchos*)	0.2–0.66	Brumm and Todt, 2002
	Budgerigars (*Melopsittacus undulatus*)	0.16	Osmanski and Dooling, 2009
	Canaries (*Serinus canaria*)	0.1	Hardman et al., 2017
	Mallard (*Anas platyrhynchos*)	0.18–0.75	Dorado-Correa et al., 2018
	Tinamou (*Eudromia elegans*)	0.75	Schuster et al., 2012
	Domestic fowl (*Gallus gallus domesticus*)	0.41	Brumm et al., 2009
Sirenians	West Indian manatee (*Trichechus manatus*)	n.s.	Miksis-Olds and Tyack, 2009

An overview of the documented Lombard response magnitude (measured as dB change in signal amplitude per dB change in noise) in mammals and birds. For both bat species, the Lombard response was measured for echolocation signals. n.s., not significant.

other primates (Brumm et al., 2004; Egnor and Hauser, 2006) as well as bats (Tressler and Smotherman, 2009) and several different bird taxa (Brumm and Todt, 2002; Cynx et al., 1998; Dorado-Correa et al., 2018). Thus, many highly vocal terrestrial animals display a Lombard response that helps to partially offset the reduction in active space, yet none of them fully compensate for increased ambient noise and, therefore, face a loss of active space during periods of increased noise.

A series of studies have examined the Lombard response in marine mammals. In 2005, Scheifele and colleagues first described a Lombard response of 0.9 dB per 1 dB increase in ambient noise in beluga whales (*Delphinapterus leucas*) (Scheifele et al., 2005). Subsequently, Lombard responses of ∼0.8–1 dB per 1 dB increase in noise have been reported for groups of killer whales (*Orcinus orca*) (Holt et al., 2009), North Atlantic right whales (*Eubalaena glacialis*) (Parks et al., 2011a,b) and humpback whales (*Megaptera novaeangliae*) (Dunlop et al., 2014; Fournet et al., 2018). Thus, cetaceans seem to almost match increases in ambient noise with increases in signal amplitude, at least within the range of ambient noise levels measured in the respective studies.

This variation in the Lombard response warrants further investigation. The acoustic communication range will decrease for animals that only partially compensate for increases in ambient noise, which can affect group cohesion, encounter rates and mate attraction (Clark et al., 2009). However, if cetaceans are able to compensate fully for increased ambient noise within a reasonable span of ambient noise levels, their active space remains constant and they only have to manage any potential energetic demands associated with increased signalling effort (Holt et al., 2015, but see also Pedersen et al., 2020).

Here, we tested the hypothesis that dolphins compensate for increasing ambient noise in a 1 dB to 1 dB manner as reported for larger cetaceans. We investigated this using acoustic tags deployed on free-ranging common bottlenose dolphins, *Tursiops truncatus* (Montagu 1821), which is one of the best-studied cetacean species because of its cosmopolitan distribution and prevalence in marine parks and aquariums (Wells and Scott, 2018). Bottlenose dolphins are known to produce individually distinctive signature whistles (Caldwell and Caldwell, 1965; Caldwell et al., 1990; Sayigh et al., 2007) that are important for facilitating group cohesion (Janik and Slater, 1998; King et al., 2016; Quick and Janik, 2012). As such, signature whistles may be especially important in situations of increased separation, especially in typically murky estuarine habitats, where maintaining active space is more critical. Therefore, we tested whether vocal amplitude compensation was different for signature and non-signature whistles.

MATERIALS AND METHODS

Study animals and location

The study was conducted with the long-term resident community of common bottlenose dolphins in Sarasota Bay, FL, USA (Wells, 2014). This is an urbanized coastal area where dolphins are exposed to a vessel passing within 100 m every 6 min on average during daylight hours (Nowacek et al., 2001). As such, this habitat involves highly fluctuating noise levels with frequent increases in masking noise (Fig. 1) within frequencies used for signature whistles (Fig. S1).

As part of a long-term study (Irvine et al., 1981; Wells, 1991), resident dolphins have been handled and examined during periodic capture–release sessions conducted since 1970, taking advantage of the shallow waters of the dolphins' range. Early efforts emphasized marking animals for future identification for behavioural studies,

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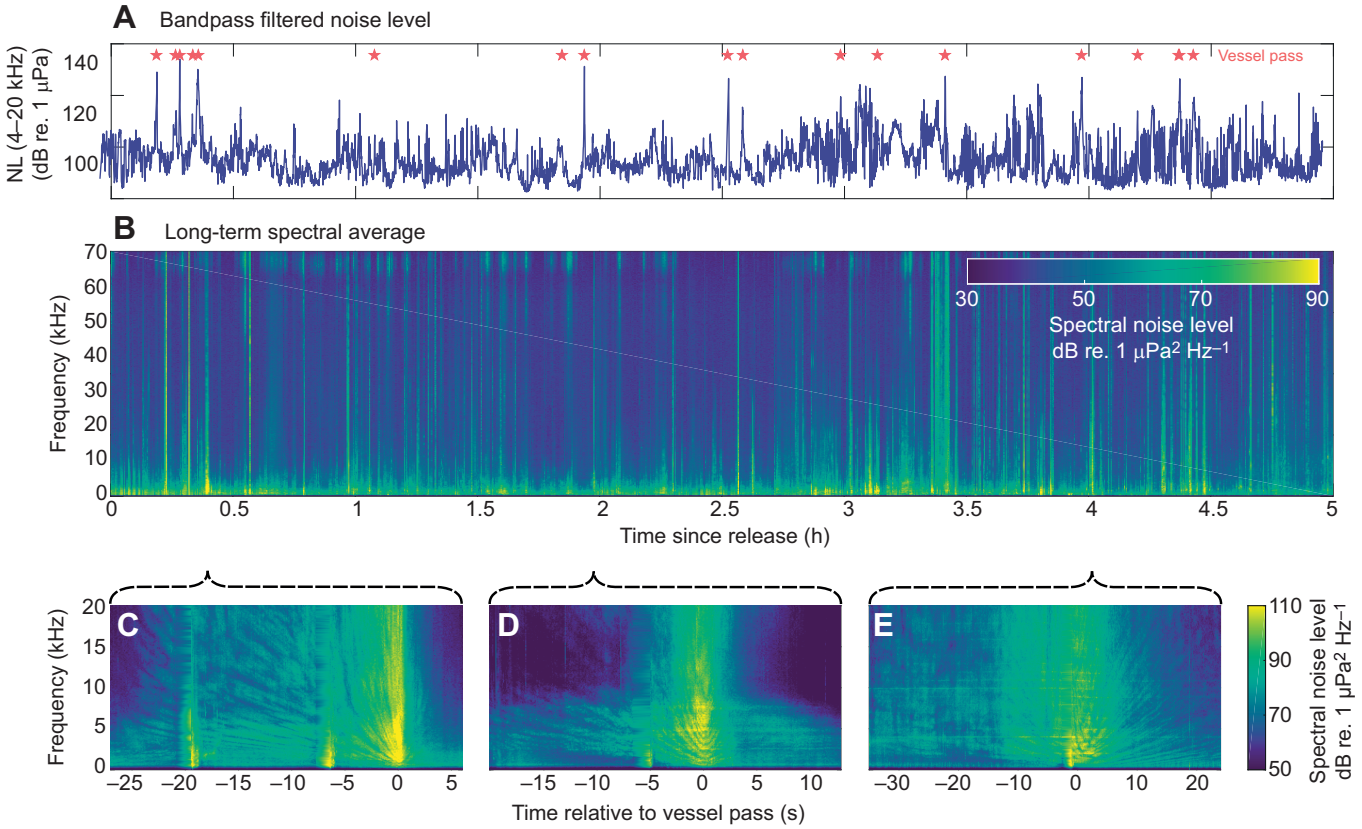

Fig. 1. Example of ambient noise exposure for a bottlenose dolphin in Sarasota Bay. (A,B) Ambient noise throughout a 5 h tagging period immediately following release, calculated as either ambient noise level (NL) within a 4–20 kHz analysis band (A) or as spectral noise level (B). Long-term spectral noise level was calculated for each 2 s block by subdividing the block into 0.1 s analysis windows with 90% overlap, identifying the analysis window with the lowest bandpass-filtered noise level, then calculating the power spectral density using Welch's method (FFT size 4096, sample rate 240 kHz). Surfacing periods within 0.2 m of the surface were identified and removed using linear interpolation of both bandpass-filtered noise level and spectral noise level. Aurally identifiable close vessel approaches were manually labelled within the dataset (red stars) and a spectrogram calculated for three example vessel passes (C–E) to show the broadband noise generated by cavitation.

and obtaining life history and genetic information on each resident dolphin to facilitate interpretation of behaviour; since 1988, health parameters have been examined as well (Wells, 2009; Wells et al., 2004). During capture–release sessions, a large seine net (500×4 m in size) was deployed from a motorboat to encircle a small group of dolphins in shallow water. Once enclosed in a net corral, experienced handlers could safely handle and support the animals. A suite of morphological, physiological and behavioural data were collected, partly in water and partly on an adjacent sampling boat with a shaded, padded deck. Behaviour and respiratory patterns were closely monitored by veterinarians throughout the process, and water was repeatedly washed over the dolphins when on deck. The whole process typically required 1–2 h, after which the dolphins were ready to be released on site.

Permits

Fieldwork was carried out under National Marine Fisheries Service Scientific Research Permit no. 15543 to R.S.W. as well as through IACUC approvals through Woods Hole Oceanographic Institution, Mote Marine Laboratory and the University of St Andrews Animal Welfare and Ethics Committee.

Experimental design

Before release, some dolphins were instrumented with a high-resolution sound and movement recording DTAG3 (Johnson and Tyack, 2003), which was positioned roughly halfway between the blowhole and the dorsal fin, approximately 0.5 m from the melon (Fig. 2A). The skin of the dolphin was gently scrubbed with a piece of paper towel to remove algae and dead skin cells, and the tag was attached with four small (approximately 48 mm diameter) sterilized suction cups. The tag continuously recorded 16-bit sound on two hydrophones at a sample rate of 240 kHz and with a flat frequency response within ±2 dB between 0.5 and 80 kHz. A pressure sensor, tri-axial accelerometer and magnetometer were sampled at 200–250 Hz after passing through an analog low-pass filter with a −3 dB cut-off frequency of one-third of the sampling rate. Preceding the experiment, tag sensitivities were measured by relative calibration in an anechoic tank (1.5 m diameter, Aarhus University) to a clip level of 179 dB re. 1 µPa (±1.2 dB between tags). The tags were programmed to release after a specified time period (up to 24 h), but many came off before this programmed release (see Table S1) as a result of high-energy activities of the dolphins, including repeated breaching, fast sprints or energetic interactions with conspecifics. After detachment, the tags floated to the surface to be retrieved using boat-based tracking of their VHF beacons with a Yagi antenna and an R1000 VHF receiver (Communication Specialists, Inc.).

Obtaining whistle parameters from tag recordings

All tag recordings were audited in MATLAB R2013b (The MathWorks, Inc., Natick, MA, USA) using DTAG-toolbox scripts (https://www.soundtags.org/). In this process, each recording was manually inspected in sequential 10 s segments. For each period,

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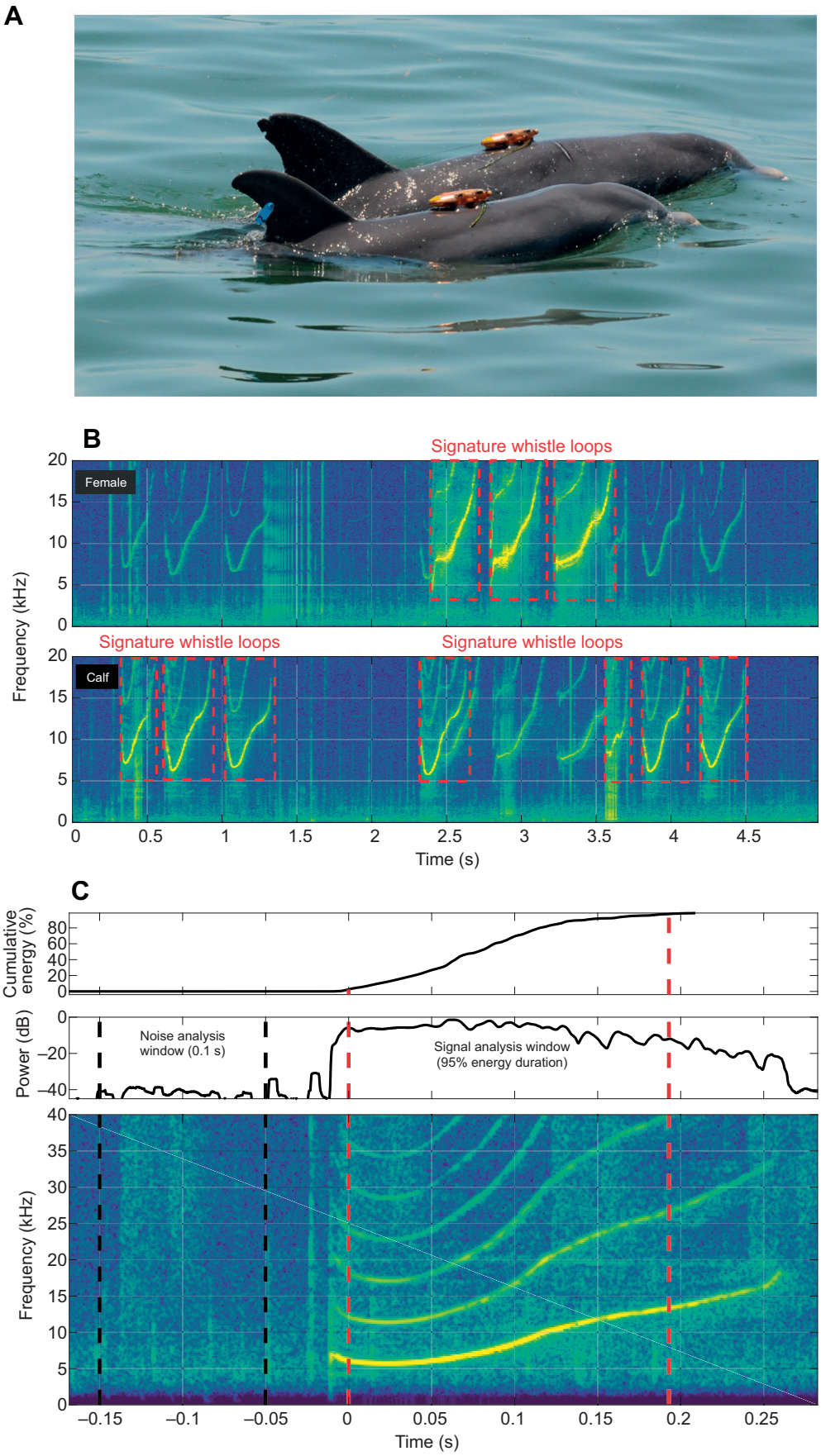

Fig. 2. Experimental study design. (A) Each dolphin in this study was instrumented with a high-resolution sound-recording DTAG (photograph taken by the Sarasota Dolphin Research Program under National Marine Fisheries Service Scientific Research Permit No. 15543). (B) Tag recordings were manually audited using simultaneous sound spectrograms to parse out vocalizations from closely associated individuals. (C) Each whistle was analysed to extract the following parameters: apparent output level (AOL, dB re. 1 µPa), measured as SPL rms within a 95% energy window (indicated by dashed red lines) received on the tag, and ambient noise level (NL, dB re. 1 µPa), measured as SPL rms for a 100 ms window (indicated by dashed black lines) preceding the whistle or manually moved (within 1 s of whistle) to avoid overlap with transients. Parameters were measured within a 4–20 kHz band reflecting the frequency of signature whistles used by individuals in this study (Fig. S1).

acoustic data were downsampled to 60 kHz, and amplitude envelopes and spectrograms (Hamming window, FFT size 512, 50% overlap, 80 dB dynamic range) were displayed in concert with a synchronized dive profile.

Individual vocalizations were labelled manually along with a start time and duration cue according to the following definitions: uninterrupted tonal sounds with a narrowband fundamental frequency were labelled as either whistles (exceeding 100 ms in duration) or chirps (durations of less than 100 ms: Caldwell and Caldwell, 1968), with chirps ignored for the purpose of this paper. Whistles produced by the tagged individual were distinguished from those of non-focal individuals based on (i) intensity comparisons between two tags deployed on tightly associated pairs (mother–calf or male alliances) and (ii) a stereo angle of arrival within ±10 deg of echolocation clicks produced by that animal.

Signature whistles of each tagged individual were identified and differentiated from non-signature whistles by comparison with the dominant whistle obtained from suction-cup hydrophone recordings during health assessments, where signature whistles account for the majority of emitted whistles (Sayigh et al., 2007). No signature whistle copies (Janik, 2000b; Tyack, 1986) were included in this study, as these are generally rare.

For the subsequent analysis, accurate measures of both whistle amplitude and ambient noise were required. Therefore, we manually removed all whistles that had overlapping extraneous sound components, such as flow noise (during high-energy activities), surfacing noise, clicks or other whistles from either the tagged individual or nearby conspecifics. All remaining whistles were analysed individually to extract a range of parameters (Fig. 2B). First, each extracted sound period was filtered with a 4–20 kHz 6-pole Butterworth filter. This frequency range adequately captured the energy in the fundamental frequency of signature whistles of the recorded animals in our study while removing low-frequency flow noise that did not overlap with dolphin signals (Fig. S1).

We first estimated the ambient noise level (NL, dB re. 1 µPa) in the 4–20 kHz band as the root-mean-square sound pressure level (SPL_{rms}) within a 100 ms window preceding each whistle: $NL=10\log_{10}(I_N)$, where the noise intensity I_N is the mean of the squared pressure values throughout the noise analysis window. If loud transients (often echolocation clicks of the tagged animal or a nearby conspecific) preceded the whistle, the background noise window was manually shifted to a period without clicks within 1–2 s before the whistle, possibly generating a small but negligible time gap between the NL and apparent output level (AOL) measurements.

We then estimated the AOL (dB re. 1 µPa) of the whistle as received on the tag (Madsen et al., 2005). To do this, we calculated a time window containing 95% of the signal energy (Fig. 2; Madsen et al., 2005). We then measured the SPL_{rms} within the 95% energy window after correcting for noise intensity: $AOL=10\log_{10}(I_S-I_N)$, where signal intensity I_S is the mean of the squared pressure values over the 95% energy window and I_N is the noise intensity as defined above. The signal-to-noise ratio was then calculated as the difference between AOL and NL. These AOL measurements enabled the subsequent analysis of relative changes in output level as a function of ambient noise.

Statistics

To investigate the effect of noise level on signal amplitude, we used a subset of whistles that were filtered to have a signal-to-noise ratio greater than 6 dB and a minimum of six signature and six non-signature whistles per individual. The former criterion was implemented because measurements of signal intensity become steadily more unreliable at increasingly small signal-to-noise ratios. Given the close proximity of the tag to the sound source, this criterion affected very few signals (5% of all recorded whistles).

We performed a linear mixed-effects analysis of the relationship between AOL and NL using the *lme4* toolbox (Bates et al., 2015) in R (http://www.R-project.org/). We modelled NL, whistle type and an interaction term between the two as fixed effects to examine their importance in explaining AOL. We accounted for differences between individuals by including a random effect on both intercept and slope for each tagged dolphin.

As a model selection method, we generated four nested models: a null model with only random effects and three extending models where each new model was identical to the previous except for the addition of a fixed effect. A stepwise likelihood-ratio test was performed to evaluate the importance of each of the fixed effects and to determine which model was best fitted to the data. We visualized the marginal effect (ignoring random factors) of NL on AOL for each whistle type using parametric bootstrapping with 1000 replicates within the *bootpredictlme4* toolbox (http://www.remkoduursma.com/post/2017-06-15-bootpredictlme4/) in R. Subsequently, we constructed a separate linear mixed-effect model for each whistle type and then tested whether NL had a significant effect on AOL using the same likelihood-ratio test, by comparison with a model without NL.

RESULTS

In total, 26 individual tag recordings of 23 different individuals were analysed for this study, including data from nine mother–calf pairs and four male alliance pairs in the years 2012–2016 (see Table S1 for the full data overview). Individual tag recordings ranged in duration from 0.58 h to 24.24 h (mean±s.d., 10.95±7.72 h), amounting to a total of 284.82 h. From these recordings, we manually audited and analysed 222.42 h (see Table S1) and identified a total of 4151 whistles with no overlapping extraneous sounds. After filtering for a signal-to-noise ratio greater than 6 dB (removing 209 whistles, equal to 5% of all whistles) and a minimum of 6 signature and 6 non-signature whistles per individual (removing 7 tag recordings with a total of 87 whistles, equal to 2% of the total), our remaining dataset for statistical treatment consisted of 19 individuals (6 mothers, 8 calves, 5 males) and a total of 3855 whistles (2750 signature and 1105 non-signature whistles). Measured NL ranged from 80 to 147 dB re. 1 µPa, while the range of AOL was from 105 to 164 dB re. 1 µPa, which is compatible with previous studies of output levels for this species (Janik, 2000a; Jensen et al., 2012; Tyack, 1986).

The linear mixed-effects model showed that the addition of NL, whistle type and an interaction term between the two factors significantly improved model fit (see ΔAIC and ΔBIC; Table 2) and that all three of these fixed effects had a significant effect on AOL (Table 2).

We found a much lower degree of amplitude compensation compared with previous studies on cetaceans, despite a large variation within individual datasets. Representative relationships between AOL and noise level are shown for both signature and non-signature whistles of a representative mother, calf and male in Fig. 3. AOL within each whistle type varied greatly, with significant variation in the estimated Lombard response magnitude across datasets (Fig. 4A,B). Despite these confounding factors, all datasets showed a Lombard response magnitude far less than the ∼0.9–1 dB per 1 dB noise found in previous cetacean studies (Table S1).

Table 2. Model selection using likelihood-ratio test

Model		d.f.	ΔAIC	ΔBIC	χ^2	*P*-value
Full model:	AOL~**NL**+**WT**+**NL**×**WT**+(*1*+*NL*|*ID*)	8	0	0	37.62	<0.0001
Model 2:	AOL~**NL**+**WT**+(*1*+*NL*|*ID*)	7	35	29	1050.22	<0.0001
Model 1:	AOL~**NL**+(*1*+*NL*|*ID*)	6	1084	1071	22.32	<0.0001
Null model:	AOL~(*1*+*NL*|*ID*)	5	1104	1085		

Four linear mixed-effects models (fixed effects in bold, random effects in italics) were tested hierarchically, with χ^2 and *P*-values for each model representing a test against the model one level down. The results show that the addition of each fixed effect significantly improved the model. Thus, all three fixed effects had a significant effect on apparent output level (AOL: dB re. 1 µPa) (*P*<0.0001). The full model showed that signature whistles were 8.6 dB higher output than non-signature whistles, with a shallower slope (0.14±0.03 dB per 1 dB noise level) compared with non-signature whistles (0.14±0.03 dB per 1 dB noise level). NL, noise level (dB re. 1 µPa); WT, whistle type; ID, individual.

We also found significant differences in the output level of signature and non-signature whistles (for the entire dataset: signature whistle mean±s.d. AOL: 133±7.5 dB re. 1 µPa, non-signature whistle AOL: 127±9.3 dB re. 1 µPa). Thus, the AOL of signature whistles was generally greater than that of non-signature whistles, with a difference of 8.6 dB after accounting for individual differences and the simultaneous effect of noise.

Finally, we found that the effect of NL on AOL was significantly lower for signature whistles (0.14±0.03 dB per 1 dB noise) than for non-signature whistles (0.32±0.03 dB per 1 dB noise). These results were robust to different acoustic measures of AOL, irrespective of whether models were run using rms output level, 200 ms peak rms level or energy flux density (Table S2). A separate linear mixed-effects model with only signature whistles demonstrated that the AOL of these whistles was significantly correlated with NL despite a low slope (χ^2_1=11.214, *P*=0.0008).

DISCUSSION

Animals that communicate acoustically need to solve the challenge of successfully transmitting signals in varying conditions of ambient noise. In this paper, we show that bottlenose dolphins demonstrate a Lombard response by adjusting signal amplitude in response to variation in ambient noise levels. We found that the magnitude of this response is consistent with studies of terrestrial species, yet much lower than reported by previous studies on larger cetaceans. Furthermore, the response magnitude was on average consistently lower for signature whistles (0.1 dB increase in AOL per 1 dB increase in NL) than for non-signature whistles (0.3 dB increase in AOL per 1 dB increase in NL), demonstrating the utility of separating signals with different functions when studying vocal compensation in wild animals.

The lower amplitude adjustments seen for signature whistles may be a consequence of these whistles inherently operating at higher output levels than non-signature whistles, rendering a smaller potential scope for the Lombard response. Similar arguments have been presented to explain why some species of frogs (Schwartz and Bee, 2013) and tokay geckos (Brumm and Zollinger, 2017) do not exhibit a Lombard response. While signature whistles were emitted on average at 9 dB higher output levels compared with non-signature whistles, this difference depended on noise level, and the two signal types gradually converged on similar output levels at high noise levels. Maximum source levels of wild bottlenose dolphins have been estimated to be approximately 162–169 dB re. 1 µPa SPL_{rms} (Janik, 2000a; Jensen et al., 2012), which is

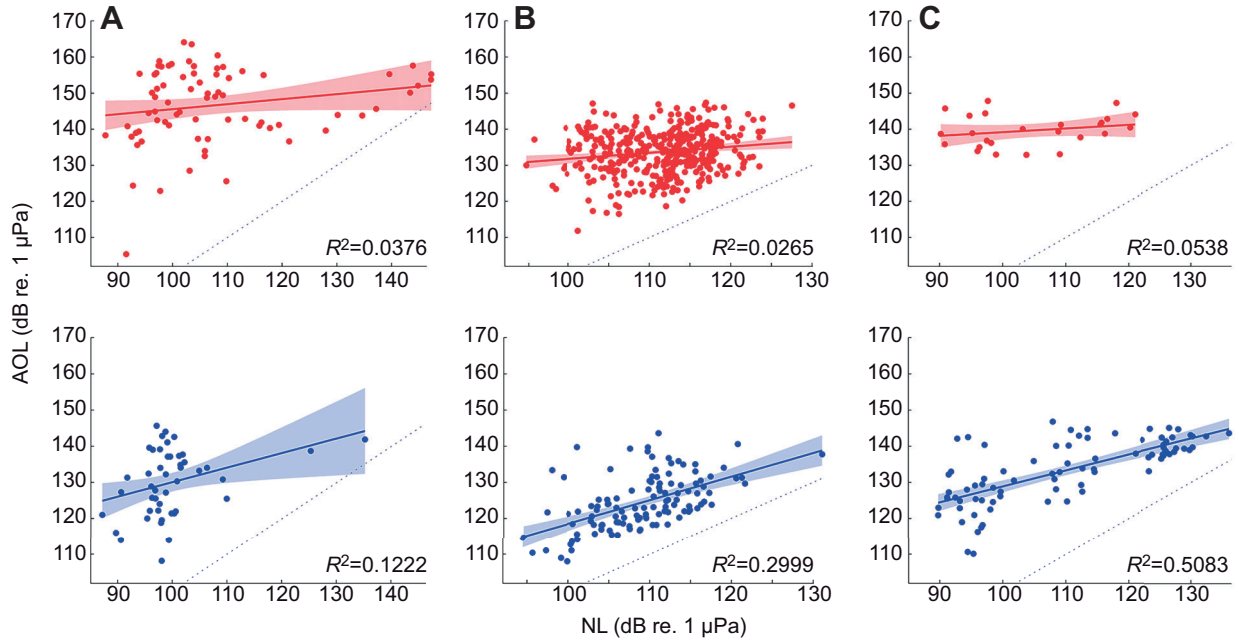

Fig. 3. Variation in amplitude adjustment to noise. The relationship between AOL and NL for signature (top row, red) and non-signature (bottom row, blue) whistles for a representative mother (A), calf (B) and male (C). Filled circles represent whistles, whereas solid line and shaded area represent a linear regression and 95% regression confidence interval. A signal-to-noise ratio where signal amplitude equals noise amplitude is shown as a dotted line in each plot.

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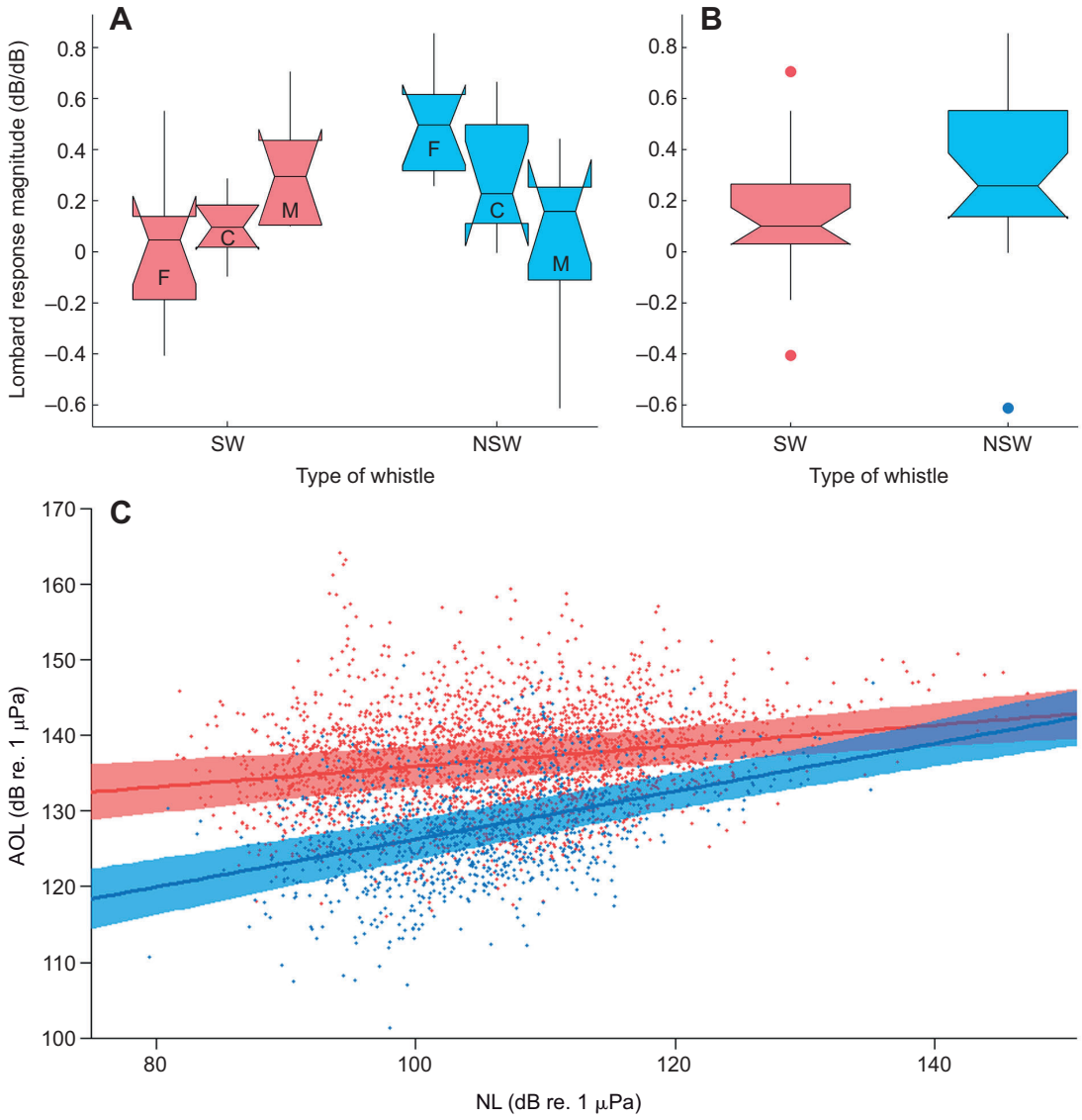

Fig. 4. Signal-specific Lombard response magnitude. (A) Boxplot showing the distribution of Lombard response magnitudes (dB whistle/dB NL) obtained from linear regression on signature whistles (SW) and non-signature whistles (NSW) for each individual animal, based on whether it was a female (F), a calf (C) or an allied male (M). (B) Boxplot showing differences between signature and non-signature whistles pooled across individuals. Slopes were generally larger for non-signature whistles (median: 0.3 dB whistle/dB NL) than for signature whistles (median: 0.1 dB whistle/dB NL) but with large variation between individuals. For both plots, boxes represent upper and lower quartiles, horizontal middle lines indicate medians, and notches represent 95% confidence interval of the median. Whiskers extend to the most extreme data point within 1.5×interquartile range (IQR), and points beyond 1.5×IQR (probably outliers) are marked as coloured circles. (C) The marginal effect (ignoring random factors) of NL (dB re. 1 Pa) on AOL (dB re. 1 µPa) for signature whistles (red) demonstrated a significantly lower Lombard response magnitude than for non-signature whistles (blue). Coloured dots represent whistles, whereas solid lines and shaded areas represent the linear mixed-effects model prediction and 95% confidence intervals.

comparable to the maximum output levels measured in this study, especially considering that tag-recorded AOLs need to be corrected for tag placement and directivity to be directly comparable with an on-axis source level at 1 m distance. Higher output levels of signature whistles are probably tied to differences in function between the two signal types. Signature whistles are used to broadcast individual identity (Sayigh et al., 1999) and facilitate group cohesion (Janik and Slater, 1998), including when separate groups meet at sea (Quick and Janik, 2012) or when mother–calf pairs need to reunite (King et al., 2016; Smolker et al., 1993). These functions are likely to benefit from a higher output level and the larger detection range that comes with it. In contrast, while much less is known about the functions of non-signature whistles, the 9 dB lower output levels for non-signature whistles would result in a threefold smaller detection range (Jensen et al., 2012; Quintana-Rizzo et al., 2006). This smaller active space supports the notion that many non-signature whistles may be used in more discreet short-range communication contexts, which could serve many potential functions (Gustison and Townsend, 2015). At the same time, the lower output levels of non-signature whistles compared with the physiological peak output levels allow a larger scope for changing amplitude in response to noise.

The Lombard response magnitudes of signature and non-signature whistles in this study are similar to those demonstrated for terrestrial mammals (Egnor and Hauser, 2006; Garnier et al., 2010; Tressler and Smotherman, 2009), but lower than shown for

other cetaceans across a similar span of noise levels (90–150 dB re. 1 µPa SPL_{rms}) (Holt et al., 2009; Parks et al., 2011a; Scheifele et al., 2005). Part of the reason for the different results might be ascribed to socio-behavioural differences among the cetacean species being studied and the contexts in which they were studied. We know from humans that the Lombard response may depend on social context as well as speaker task (Garnier et al., 2010; Lu and Cooke, 2008), though this is less well understood for animals. One study of Bengalese finches found a Lombard effect in undirected song but not in directed singing (Kobayasi and Okanoya, 2003), but the evidence was inconsistent across individuals, and several other studies of the closely related zebra finch have found a Lombard response during undirected singing (Cynx et al., 1998; Zollinger et al., 2011). In this study, all tagged dolphins were closely associated pairs, either mothers with a dependent calf or allied males (Connor and Krützen, 2015; Wells, 2003). It is possible that the majority of the recorded whistles were exchanges between the tagged individuals and, thus, used in relatively short-range communication where range was not limited by noise. Studies on this dolphin population have shown that pairs often stay within communication range of each other while moving through their acoustically complex habitat (Quintana-Rizzo et al., 2006), which might lessen the motivation to maintain their active space and lead to a smaller Lombard response if this is cognitively modulated. At the same time, animals might change overall cohesion in response to increasing noise (Buckstaff, 2004), thus offsetting the need to increase vocal output. It is possible that communication within larger social groups or with distant conspecifics is more sensitive to changes in detection range, necessitating a tighter coupling of signal output level and noise level. However, this argument breaks down for animals communicating to distant animals at an unknown range, where a better option may just be to vocalize as loudly as possible.

There are several methodological differences between studies that may also help explain our different results. Studies of the Lombard response require reliable measurements of both signal output levels and any simultaneous changes in background noise (or experimentally manipulated noise), but this is quite difficult to obtain for cetaceans in the wild. Scheifele et al. (2005), Holt et al. (2009) and Dunlop et al. (2014) used hydrophone arrays to obtain estimates of output levels of whale signals and concurrent fluctuations in noise levels. This method has two problems. First, the spatial offset between the animals and the hydrophone means that the noise level experienced by the animals may be considerably different from the noise level recorded. While this problem may be less important in the case of noise generated primarily by wind and waves rather than shipping (Dunlop et al., 2010), changes in depth of the whale or bathymetry at and around the location of the whale still affect the resulting noise level. Second, because the signal-to-noise ratio of each signal has to be sufficiently high to enable a reliable measurement of the signal, this method also biases analysed signals toward higher amplitude signals. As signal-to-noise ratio also depends on transmission range, this filtering introduces a further bias towards higher amplitude signals (or signals recorded at shorter range) at higher ambient noise levels, thus potentially driving a larger apparent vocal adaptation to noise.

On-animal tag recordings (Parks et al., 2011a; this study) offer some advantages with respect to both of these issues. If calls from the tagged individual can be determined confidently, the spatial offset between noise recorded and noise experienced by the animals is minimal, as estimates of concurrent noise levels can be recorded at the location of the animal. At the same time, signals are recorded at a constant distance close to the sound-production apparatus of the animal and at a relatively high received level compared with more distant recordings. However, there are still some difficulties for recording signals on the tag. These tags are almost always positioned behind the sound generator and, as a consequence, signal features received on tags are likely to be different from those that would be recorded at 1 m in front of the animal, i.e. the source level (Johnson et al., 2009). However, because of the relatively omnidirectional nature of the fundamental frequency of bottlenose dolphin whistles (Branstetter et al., 2012), any relative changes in AOL will probably mirror changes in source level. Another problem is flow noise from animal movement on tags. We were able to eliminate flow noise by excluding noise below 4 kHz. This is justified because the main noise sources were small boat engines that produce considerable high-frequency noise (Fig. 1), because whistles do not contain energy below 4 kHz (Fig. S1), and because dolphin hearing sensitivity is poor at low frequencies (Johnson, 1968). This problem would be harder to solve in an area where most noise comes from large vessels producing primarily low-frequency noise and where animals communicate and hear in those lower frequency bands, as is the case for large whales.

Furthermore, when using tags to assess noise-dependent vocal adjustments, the experimental design has to ensure that signals produced by the tagged individual can be readily discerned from signals from other individuals – even at very close range. In this study, we used stereo angle-of-arrival estimates and amplitude comparisons between pairs of tagged animals to accomplish this, with known signature whistles of tagged individuals providing additional certainty. A corresponding level of certainty is more difficult to accomplish in studies of the larger baleen whales. Acoustic signals generated by baleen whales are low frequency and can propagate over relatively large distances, which makes it challenging to ensure that signals are from the tagged animal. While Parks et al. (2011a,b) minimized this problem by visually ensuring that the tagged animal was alone at the surface, other studies have used high-resolution accelerometers on tags to detect low-frequency vibrations on the surface of fin whales as an indication of vocal activity (Goldbogen et al., 2014), which might be an interesting method for future studies of vocal amplitude compensation in large cetaceans. Similarly, clicks from tagged animals are often much easier to identify because of their off-axis distortion, and thus species that communicate with click-based signals, such as some delphinids (Pérez et al., 2016) or narrow-band high-frequency species (Martin et al., 2018; Sorensen et al., 2018), may be good species in which to examine Lombard response magnitude.

The lower Lombard response magnitude found in this study is important to consider in the assessment of how anthropogenic noise may affect acoustic communication, as it means that animals will experience a loss of active space during periods of increased ambient noise. Decreases in potential communication range can be estimated in situations when noise levels, sound propagation conditions and source characteristics of communication signals are known or measured (Jensen et al., 2009). Several studies have modelled changes in detection range as a consequence of large-scale and long-term anthropogenic noise in marine environments, aiming both to understand contributions of different noise sources and to decrease impacts through improved management (Clark et al., 2009; Hatch et al., 2012). However, none of these models account for potential compensatory mechanisms and thus they may be overestimating loss of communication space. In the long run, these efforts may help us evaluate long-term population-level effects of anthropogenic noise (Nabe-Nielsen et al., 2014; New et al., 2014) and thus enable better data-driven conservation and marine planning

(Hatch et al., 2016). However, there are still many poorly understood aspects of acoustic masking, such as the extent of spatial release from masking (Erbe et al., 2016b), or potential compensation mechanisms that should be incorporated into models of masking.

Conclusion

In this study, we have shown that bottlenose dolphins partially compensate for increased noise by adjusting signal amplitude, with higher output levels and lower compensation for signature whistles that are associated with group cohesion than for non-signature whistles of unknown function. These findings underline the need for further investigations of the interaction between signal types, masking and how the social function of calls may be used to predict range of communication. Further studies are needed to investigate how dolphins modulate the intensity of their whistles in order to tailor their effective range to the function of the whistle, varying noise levels and varying propagation loss in different habitats such as the sand flats, open bays and sea grass meadows (Quintana-Rizzo et al., 2006). These analyses are required to understand and evaluate socio-behavioural consequences of increased noise, including maintenance of contact between mother and calf, changes in overall structure and connectivity of a fission–fusion society, decreased encounter rates with conspecifics, lost mating opportunities, and possible shifts in time and energy budgets, as potential consequences of behavioural compensation mechanisms.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: I.M.K., F.H.J.; Methodology: F.H.J.; Software: F.H.J.; Formal analysis: I.M.K.; Investigation: I.M.K., K.M., R.S.W., L.S.S., V.M.J., P.L.T.; Resources: K.M., R.S.W., L.S.S., V.M.J., P.L.T.; Data curation: I.M.K.; Writing - original draft: I.M.K.; Writing - review & editing: I.M.K., K.M., R.S.W., L.S.S., V.M.J., P.L.T., F.H.J.; Visualization: I.M.K., F.H.J.; Supervision: F.H.J.; Project administration: I.M.K., F.H.J.; Funding acquisition: R.S.W., P.L.T., F.H.J.

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Supplementary information

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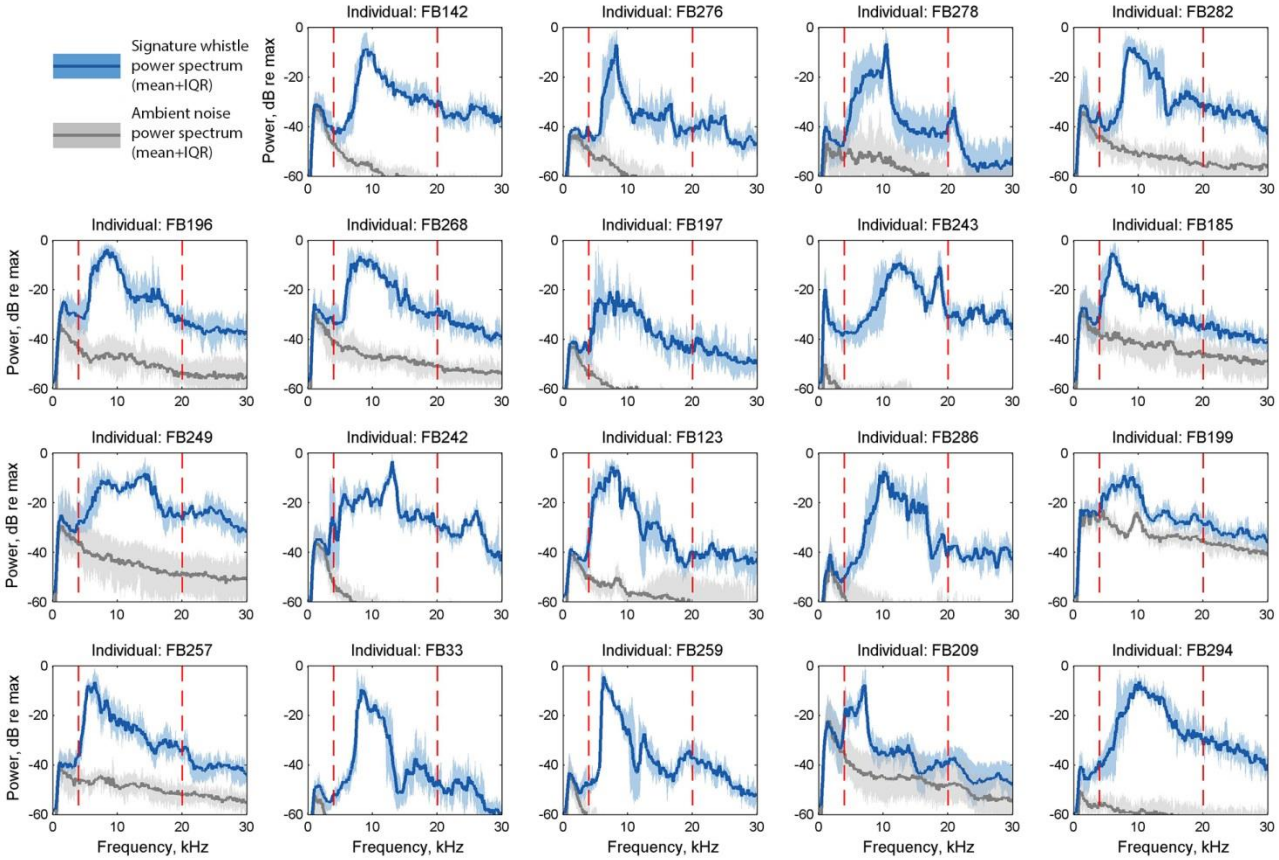

Figure S1 – Spectral energy distribution of bottlenose dolphin signature whistles used for estimating Lombard response magnitude. Ten signature whistles for each individual were extracted and filtered with a 1 kHz to 80 kHz 6-pole Butterworth filter, after which a calibrated power spectral density (PSD) estimate was obtained using the Welch method (240 kHz sample rate, 4096 Hamming window, 50% overlap) for both the signal (95% energy duration) and a 0.1s noise segment preceding the whistle. Blue line represents the mean power spectral density estimate of signature whistles after each PSD was normalized to peak PSD. Grey lines represent the mean power spectral density estimate of the preceding noise segment after each PSD was normalized to the peak PSD of the subsequent signature whistle. Shaded areas represent interquartile range, and red lines indicate analysis band in present study.

					Raw data		Whistle analysis					Linear regression	
Year	*Tag ID*	*Animal ID*	*Type*	*Age*	*Recording time (h)*	*Analysis duration (h)*	*SW*	*NSW*	*HQ SW*	*HQ NSW*	*HQ total*	*SW slope (R^2)*	*NSW slope (R^2)*
2016	128a	FB33	Mother	34	24,24	12,00	135	94	71	21	92	0,06 (0,02)	0,59 (0,28)
	128b	F259	Calf (f)	3	24,21	5,10	2362	356	942	81	1023	0,10 (0,05)	0,34 (0,11)
	131a	F209	Mother	12	6,30	6,30	37	21	10	14	24	0,03 (0,00)	0,32 (0,10)
	131b*	F255	Calf (f)	3	6,30	6,30	20	3	9	1	10	-	-
	132c*	F223	Mother	15	0,58	0,58	21	1	14	0	14	-	-
	132d	F294	Calf (m)	3	18,35	18,35	504	391	349	173	522	0,03 (0,00)	0,09 (0,01)
2015	131a	F123	Mother	17	20,50	16,00	58	95	31	54	85	-0,19 (0,04)	0,62 (0,53)
	131b	F286	Calf (m)	3	20,50	16,00	892	385	518	228	746	0,29 (0,06)	0,67 (0,34)
	134a	F199	Mother	13	17,84	12,21	44	89	11	21	32	0,55 (0,42)	0,26 (0,17)
	134b	F257	Calf (f)	2	18,17	12,02	619	276	405	135	540	0,17 (0,03)	0,65 (0,30)
2014	125a	F196	Male	16	10,61	10,61	128	120	24	41	65	0,29 (0,17)	0,19 (0,05)
	125b	F268	Male	21	8,86	8,86	75	29	29	15	44	0,35 (0,39)	0,06 (0,00)
	126a*	F276	Male	22	2,28	2,28	35	38	11	6	17	-	-
	126b*	F142	Male	22	9,62	9,62	159	132	6	5	11	-	-
	127a	F197	Mother	11	18,23	18,23	252	124	92	46	138	0,14 (0,04)	0,40 (0,12)
	127b	F243	Calf (f)	2	18,18	18,18	548	101	222	35	257	0,00 (0,00)	0,22 (0,09)
	129a	F185	Mother	14	4,75	4,75	180	85	7	13	20	-0,41 (0,13)	0,86 (0,27)
	129b	F249	Calf (f)	3	21,01	21,01	767	427	102	44	146	0,20 (0,01)	0,23 (0,06)
	129c*	F164	Male	25	1,48	1,48	11	53	3	25	28	-	-
	129d	F242	Male	24	5,71	5,71	49	269	25	86	111	0,10 (0,05)	0,44 (0,51)
2013	130a*	FB33	Mother	31	5,31	2,90	12	59	0	5	5	-	-
	130b	F282	Calf (m)	5	2,89	2,87	48	112	19	38	57	-0,10 (0,02)	0,13 (0,05)
2012	130a	F142	Male	20	6,53	2,79	75	17	17	11	28	0,11 (0,02)	0,16 (0,03)
	130b	F276	Male	20	6,82	2,79	26	38	10	13	23	0,71 (0,27)	-0,61 (0,24)
	132a	F278	Calf (m)	2	2,74	2,74	153	439	10	98	108	0,10 (0,08)	0,00 (0,00)
	132b*	FB07	Mother	28	2,81	2,74	4	5	3	2	5	-	-

Table S1: Overview of source data and estimated Lombard response magnitude per dataset. SW = signature whistle, NSW is non-signature whistle (confirmed using Sarasota Dolphin Signature Whistle Database); Recordings with * were excluded from statistical analysis since they had less than 6 high-quality whistles in one or both whistle categories

Table S2 – Results were robust to specific measures of apparent output level. The full linear mixed-effects model (fixed effects in bold, random effects in italic) was regenerated for three different AOL measures: An RMS measure across the 95% energy duration of the signal (AOL: units of dB re. 1µPa; data presented in full manuscript); the highest RMS level across a 200-ms window reflecting the integration time of low-frequency tonal signals in bottlenose dolphins (AOL_{200}: dB re. 1µPa); and an energy flux measure that accounts for changes in signal duration (AOL_{EFD}: dB re. 1µPa^2s). Apparent output level differences between signature and non-signature whistles were similar, and there were no marked differences in Lombard response magnitude (dB whistle/dB NL). *Model input abbreviations: AOL = apparent output level (dB re. 1µPa SPL_{RMS}), AOL_{200} = maximal apparent output level for a 200 ms window (dB re. 1µPa SPL_{RMS}). AOL_{EFD} = apparent output level energy flux density (dB re. 1µPa^2s), NL = noise level, WT = whistle type, ID = individual.*

Model	Δ AOL	Lombard response magnitude (dB/dB ± S.D.)	
		Signature	Non-signature
AOL ~ **NL** + **WT** + **NL*WT** + (*1+NL* | *ID*)	8.6	0.14 ± 0.03	0.32 ± 0.03
AOL_{200} ~ **NL** + **WT** + **NL*WT** + (*1+NL* | *ID*)	9.7	0.13 ± 0.03	0.33 ± 0.03
AOL_{EFD} ~ **NL** + **WT** + **NL*WT** + (*1+NL* | *ID*)	11.1	0.12 ± 0.03	0.34 ± 0.03